# Successional change in species composition alters climate sensitivity of grassland productivity

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## Abstract

Succession theory predicts altered sensitivity of ecosystem functions to disturbance (i.e., climate change) due to the temporal shift in plant community composition. However, empirical evidence in global change experiments is lacking to support this prediction. Here, we present findings from an 8-year long-term global change experiment with warming and altered precipitation manipulation (double and halved amount). First, we observed a temporal shift in species composition over 8 years, resulting in a transition from an annual $C_3$-dominant plant community to a perennial $C_4$-dominant plant community. This successional transition was independent of any experimental treatments. During the successional transition, the response of aboveground net primary productivity (ANPP) to precipitation addition magnified from neutral to +45.3%, while the response to halved precipitation attenuated substantially from −17.6% to neutral. However, warming did not affect ANPP in either state. The findings further reveal that the time-dependent climate sensitivity may be regulated by successional change in species composition, highlighting the importance of vegetation dynamics in regulating the response of ecosystem productivity to precipitation change.

## 1 INTRODUCTION

Long-term shift in the sensitivity of ecosystem functions to climatic change (Smith, Knapp, & Collins, 2009) has been widely supported with empirical evidence (Fu et al., 2015; Melillo et al., 2002; Piao et al., 2017; Wu, Dijkstra, Koch, & Hungate, 2012; Yvon-Durocher, Hulatt, Woodward, & Trimmer, 2017). Multiple mechanisms have been proposed for causing the altered climate sensitivity of ecosystem functions. Among them are organism acclimation (Bradford et al., 2008; Crowther & Bradford, 2013; Smith, Malyshev, Shevliakova, Kattge, & Dukes, 2016), substrate depletion (Luo, Wan, Hui, & Wallace, 2001; Melillo et al., 2002), nutrient and species diversity loss (Wu et al., 2012) underlying the dampened sensitivity over time; and species compositional change responsible for the amplified sensitivity over time (Wilcox, Blair, Smith, & Knapp, 2016; Xu et al., 2015). Ecological theory also predicts that ecosystem responses to perturbation (such as climate change) vary with successional states (Odum, 1969) and dynamic vegetation composition driven by succession may modulate ecosystem responses to climate change.

Cross-site experiments have suggested that plant communities at different successional states respond differently to climate change. Kröel-Dulay et al. (2015) showed that plant species richness and composition were responsive to experimental warming or drought in three early successional European shrublands, but were resistant in mature shrubland ecosystems, along a large climatic gradient. Similarly, Grime et al. (2000) reported that plant community biomass and composition in an early successional fertile limestone grassland showed greater responses to experimental warming and drought than those in a late-successional infertile grassland. These findings suggest that differences in plant functional groups, resulting from differences in species composition, along successional states be a key underlying mechanism for the differential responses to climate change. However, climatic and edaphic variables often covary with the successional states in these cross-site experiments, which make these conclusions and the role of functional groups in regulating climate sensitivity elusive.

Old field succession is a form of secondary, ecological succession occurring on abandoned agricultural land. As the old field succession proceeds, the plant communities differ in several ways. Early successional communities consist of annual weedy grasses and forbs such as ragweed (*Ambrosia*) and crabgrass (*Digitaria*), and the following communities at a later stage are dominated primarily by perennial bunch grasses replacing the annual pioneer species (Booth, 1941; Davidson, 1993). Major mechanisms driving the succession are known to be resource limitation through which changes in nitrogen availability alter species competition, and aboveground vertebrate grazing (Bardgett & Wardle, 2003; Davidson, 1993; Pickett, Collins, & Armesto, 1987). In addition, shift in plant functional group (e.g., $C_3$ and $C_4$ photosynthetic pathways) may be associated with the successional change due to the possible change in nitrogen availability (Ellery, Ellery, & Verhagen, 1992). In contrast, disturbance such as herbivory, grazing and fire

may sometimes delay vegetation succession and thus maintain plant community at the earlier successional stage (Davidson, 1993).

Physiological properties of plant functional groups may determine ecosystem responses to climate change. For example, species with $C_4$ photosynthetic pathways are typically more sensitive to warming and better adapted to dry conditions than species with $C_3$ photosynthetic pathways (Ehleringer, Cerling, & Helliker, 1997; Lambers, Chapin, & Pons, 1998). The ecological advantage of $C_4$ over $C_3$ species under warmer temperature and drought is due to the fact that $C_4$ photosynthesis has a highly efficient $CO_2$ pump that elevates $CO_2$ concentration in the bundle sheath cell (Lambers et al., 1998). Findings from global change experiments (Hoover, Knapp, & Smith, 2014; Morgan et al., 2011; Niu, Sherry, Zhou, Wan, & Luo, 2010; Taylor et al., 2014; Wilcox, Von Fischer, Muscha, Petersen, & Knapp, 2015), isotope data analyses (Ehleringer et al., 1997; Von Fischer, Tieszen, & Schimel, 2008), and large-scale model predictions (Cramer et al., 2001; Epstein et al., 2002) have demonstrated that in general (a) climate warming favors $C_4$ plant species over $C_3$, (b) drought adversely affects $C_3$ plant species over $C_4$ species, and (c) increased precipitation enhances $C_4$ plant growth to a greater magnitude than $C_3$ plant growth due to higher photosynthetic water use efficiency (Knapp & Medina, 1999; Lambers et al., 1998). However, the physiological differences between the two functional groups may not translate simply into ecological responses due to the indirect effects by climate change. For example, altered soil moisture by climate change can have an indirect effect on plant growth and therefore may counteract the physiological response of plant functional groups (Mueller et al., 2016); altered plant phenology and biotic competition by climate change may also add another level of complexity to the overall ecosystem responses (Niu & Wan, 2008; Reyes-Fox et al., 2014; Shi et al., 2015). For example, warming-induced advancement of spring phenology for certain species may have a positive influence on their competitive ability (Parmesan, 2007).

Here, we leverage an 8-year (2009–2016) global change experiment in a grassland in central Oklahoma, USA where plant dominance of the ecosystem shifted from $C_3$ to $C_4$ species after the removal of grazing. This experiment was a factorial manipulation of temperature (+3°C) using infrared heaters and precipitation (halved and double amount) using rainout facility (Xu et al., 2016). Using this unique opportunity, we investigate whether the magnitude of responses of ecosystem productivity to climate change treatments (warming and altered precipitation regime) vary with successional states and whether shift in plant functional group composition can explain the temporal variation in these responses. Previous studies at this experimental site showed a lack of climate change effect on productivity in a relative short term (Xu et al., 2016). Taking advantage of all the 8-year data and a successional change in species composition, we show altered climate sensitivity of aboveground net primary productivity (ANPP) in the two distinct compositional states of plant functional groups. Specifically, we

hypothesized that due to the temporal shift in functional group composition (a) the effects of precipitation and warming treatments on ANPP would change through time, (b) the positive responses of ANPP to warming and double precipitation would amplify, and (c) the negative response of ANPP to halved precipitation would dampen over time.

## 2 MATERIALS AND METHODS

### 2.1 Study site

The experiment was conducted in a grassland on the Kessler Atmospheric and Ecological Field Station in central Oklahoma, USA (34°59′N, 97°31′W). The study site is an abandoned field from cropping. In 2008, we installed fencing around the experimental site to exclude large ungulate grazers; previously, this site had been grazed by cattle at moderate intensities for 40 years until 2008 (Xu et al., 2016). The grassland was dominated by $C_3$ grass *Bromus japonicus* Thunb., $C_3$ forbs *Ambrosia trifida*, *Apocynum sp*., *Solanum carolinense*, *Vernonia baldwinii, Securigera varia*, *Euphorbia dentate,* and $C_4$ grass *Tridens flavus*, *Sorghum halepense*. Mean annual temperature was 16.3°C with a monthly mean temperature of 4.4°C in January and 27.7°C in July, and mean annual precipitation is 914 mm (Oklahoma Climatological Survey, Norman, OK, USA). The soil texture class is loam with 51% of sand, 35% of silt and 13% of clay. The soil bulk density is 1.2 g/cm$^3$. The concentrations of soil organic matter and total *N* are 1.9% and 0.1%, respectively.

### 2.2 Experimental design

The experiment used a paired factorial design with manipulation of air temperature and precipitation (Xu, Sherry, Niu, Li, & Luo, 2013; Xu et al., 2016). There were two levels for warming: ambient temperature and elevated temperature, and three levels for precipitation: ambient precipitation, double precipitation (2 × ambient) and halved precipitation (1/2 ambient). There were four random blocks, and within each there was one experimental plot (size 2.5 m × 3.5 m) for each factorial combination of warming and precipitation treatments ($N = 24$). For the warming treatment, the experimental plot was subjected to continuously warming by an infrared heater (100 W/m$^2$; Kalglo Electronics Inc, Bethlehem, PA, USA) hung 1.5 m above the ground in July 2009, while the other plot, equipped with a 'dummy' heater, served as a control. The distance between the warmed and control plots was approximately 5 m. For precipitation treatments, we applied a year-round rainfall-collection-redistribution device as described by Zhou, Sherry, An, Wallace, and Luo (2006) with the same area of the plot to double precipitation and a rainout facility as described by Yahdjian and Sala (2002) to halve precipitation. In brief, the rainout facility design is a fixed-location facility with a roof (3.66 m × 3 m) consisting of 18 strips (3.66 m long, 8.25 cm wide, 2.5 mm thick) of transparent acrylic which can block about half of the rainfall while minimally affecting other environmental variables. The lower side of the rainout facility tilts toward the prevailing

upwind direction. The middle of the roof is 1.5 m tall. Each 2.5 m × 3.5 m plot is divided into two 2.5 m × 1.75 m subplots. Plants were clipped in the southern 2.5 m × 1.75 m subplots which are at the opposite site of the prevailing upwind direction. Lateral water movement was prevented by inserting fiberglass sheet into the ground to a depth of 120 cm. In the control plots, we installed 'dummy' frames of the rain facility. Therefore, the six treatments are control (ambient) temperature and control precipitation (CC), control temperature and double precipitation (CD), control temperature and halved precipitation (CH), warming and control precipitation (WC), warming and double precipitation (WD), and warming and halved precipitation (WH).

### 2.3 Soil temperature, soil water content, and precipitation measurements

Soil temperature was measured by thermocouples at a depth of 7.5 cm in the center of each plot. The thermocouples were connected to a CR10 datalogger (Campbell Scientific Inc., Logan, UT, USA) and recorded soil temperature every 15 min. Volumetric soil water content (v/v %) was measured once or twice a month using portable Time Domain Reflectometry equipment (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) at a depth of 1–15 cm. Precipitation data were obtained from an Oklahoma Mesonet Station (Washington Station) located approximately 200 m away from our experimental site.

### 2.4 Measurement of ANPP and its functional group biomass

Aboveground net primary productivity, separated into $C_3$ and $C_4$ species, was directly measured by annually clipping at peak biomass (usually in September) in each plot. The clipped biomass was oven-dried at 70°C for 48 hr and weighed to calculate ANPP and its function group biomass.

### 2.5 Statistical analyses

Before statistical analyses, the data were subjected to the Shapiro–Wilk test for normality and to the Levene's test for homogeneity of variance. We used repeated-measures analysis of variance (ANOVA) to examine the main and interactive effects on soil temperature, soil water content, ANPP and its functional group biomass with warming and precipitation as main effects, year as the repeated factor, and block as a random effect. Multiple comparisons were conducted based on estimates of least square means to explore the difference among the three precipitation scenarios.

Linear regression was used to detect linear trends in $C_3$ and $C_4$ biomass, and to identify the relationship between $C_3$ and $C_4$ biomass. A general mixed-effect model was constructed with warming as the fixed factor and covarying variables including annual mean air temperature, annual precipitation and annual mean functional composition (i.e., $C_4$ proportion) across time to explore the drivers of the interannual variability in the natural log response ratio (Ln rr) of ANPP to precipitation treatments. All statistical analyses were conducted in SAS v.8.1 (SAS Institute Inc., Cary, NC, USA).

# 3 RESULTS

## 3.1 Environmental conditions

Mean annual air temperature over the experimental period (2009–2016) was 16.5°C with the range of 15.3–17.9°C and mean annual precipitation was 911 mm with the range of 549–1,605 mm (Figure S1). There were no temporal trends in annual air temperature and annual precipitation over the 8-year experimental period (Figure S1). Warming and precipitation treatments had substantial effects on soil temperature and water content (Figure 1; Table S1). Eight-year warming increased soil temperature by 3°C on average and decreased soil water content by ca. 1.3% (absolute) with significant effect starting from 2013 (Figure 1a; Table S1). Halved precipitation significantly increased soil temperature by 0.6°C; precipitation treatments affected soil water content such that double precipitation increased soil water content by ca. 1% (absolute) and halved precipitation decreased soil water content by ca. 0.6% (absolute) with significant effect starting from 2012 (Figure 1b; Table S1). Warming and precipitation treatments did not interact to affect soil temperature or soil water content.

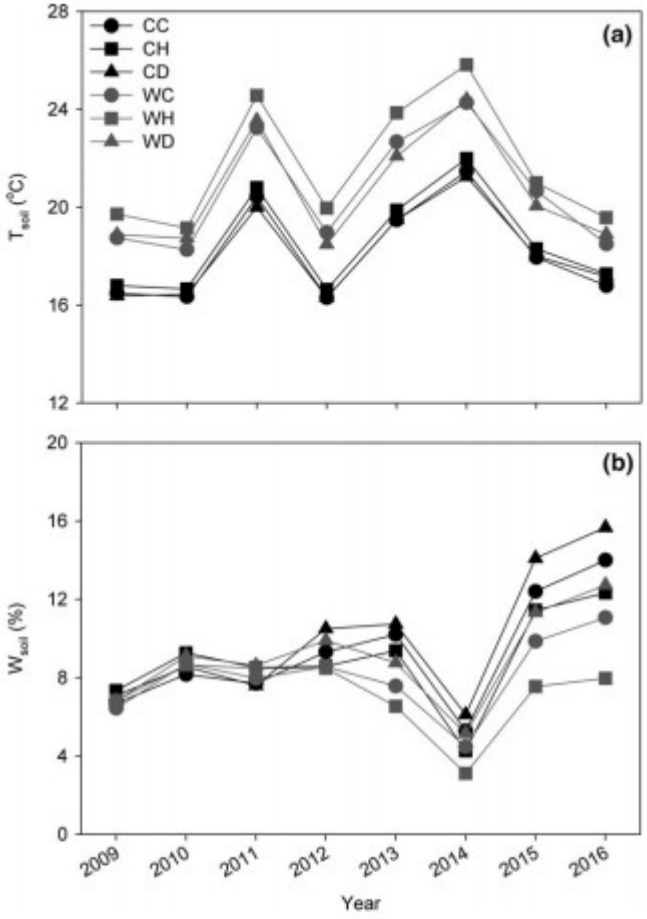


**FIGURE 1** Responses of soil temperature (ST) and volumetric soil water content (SWC) to climate change within 2009–2016. Standard errors were omitted for clarity. Eight-year warming increased soil temperature by 3°C on average, and halved precipitation significantly increased soil temperature by 0.6°C (a). Warming decreased soil water content by ca. 1.3% (absolute) with significant effect starting from 2013. Precipitation treatments affected soil water content with double precipitation increasing soil water content by ca. 1% (absolute) and halved precipitation decreasing soil water content by ca. 0.6% (absolute) with significant effects starting from 2012 (b). Warming and precipitation change did not interact to affect soil temperature or soil water content. The six treatments are control (ambient) temperature and control precipitation (CC), control temperature and double precipitation (CD), control temperature and halved precipitation (CH), warming and control precipitation (WC), warming and double precipitation (WD), and warming and halved precipitation (WH). See Table S1 for statistics

### 3.2 Temporal change in functional group biomass and composition

From 2009 to 2016, $C_3$ biomass gradually decreased ($F_{1,190} = 136.9$, $p < 0.0001$, $R^2 = 0.42$), and $C_4$ biomass increased ($F_{1,190} = 37.45$, $p < 0.0001$, $R^2 = 0.16$) to compensate the loss of $C_3$ biomass in the control plots (Figure 2a). These trends in functional group biomass were independent of warming (Figure S2) or precipitation treatments

(Figure S3). An abrupt change in functional group composition occurred in 2014 (Figure 2b). As a result, there were two distinct states of functional group composition through time: a $C_3$-dominated state from 2009 to 2013 (proportion of $C_3$ biomass: 71.0% on average over the 5 years) and a $C_4$-dominated state from 2014 to 2016 (proportion of $C_4$ biomass: 78.3% on average over the 3 years) (Figure 2b). $C_3$ biomass is negatively associated with $C_4$ biomass in all the experimental plots ($F_{1,190} = 77.67$, $p < 0.0001$, $R^2 = 0.29$; Figure 3). A typical old field successional change in species composition was associated with the functional group shift. The community transitioned from annual weedy grasses (e.g., *Bromus japonicus*) and annual forbs (e.g., *Ambrosia trifida*) to mostly perennial bunchgrass (e.g., *Tridens flavus* and *Sorghum halepense*).

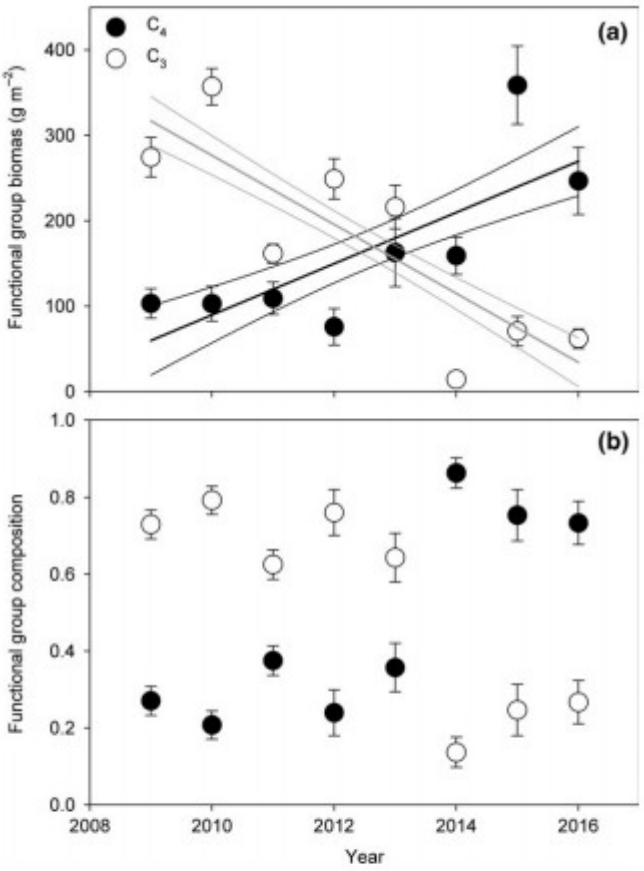


**FIGURE 2** Temporal trends in functional group biomass and composition. $C_3$ biomass (open circles) decreased linearly over time ($F_{1,190} = 136.9$, $p < 0.0001$, $R^2 = 0.42$) and $C_4$ biomass (solid circles) increased linearly over time ($F_{1,190} = 37.45$, $p < 0.0001$, $R^2 = 0.16$); gray and black lines show linear fit with 95% confidence interval (a); $C_3$ (open circles) and $C_4$ proportion (solid circles) showed a drastic shift in 2014, with a sharp decrease in $C_3$ proportion and increase in $C_4$ proportion (b). Each point represents mean and standard error of the mean across all control experimental plots ($n = 4$)

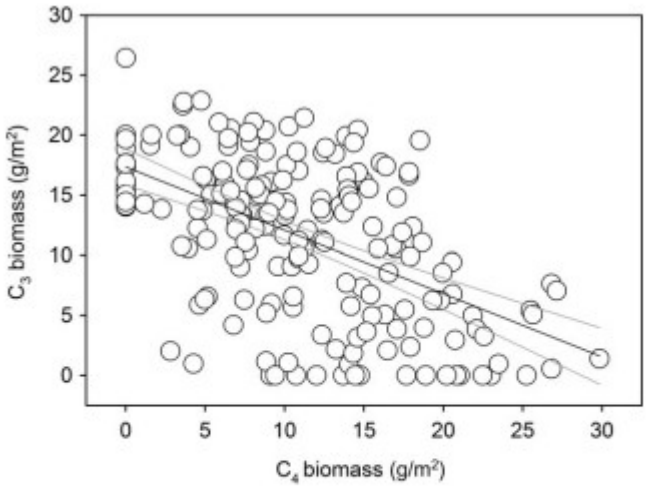


**FIGURE 3** The correlation between functional group biomass. The negative correlation between $C_3$ biomass and $C_4$ biomass ($F_{1,190} = 77.67$, $p < 0.0001$, $R^2 = 0.29$) was observed. The original data were square-rooted. Data in all treatments were included within 2009–2016 ($n = 192$). Gray line shows linear fit with 95% confidence interval

### 3.3 Responses of total ANPP and functional group biomass to climate change

Given the compositional state shift in the two functional groups, we evaluated the effects of precipitation and warming treatments on ANPP and the functional group biomass (i.e., $C_3$ and $C_4$) in the two states within 2009–2013 and 2014–2016, respectively. Double precipitation did not affect ANPP in the first compositional state ($C_3$-dominated community), but increased ANPP by an average of 45.3% in the second compositional state ($C_4$-dominated community; Figure 4a,b; Table 1). Halved precipitation reduced total ANPP in the first compositional state by an average of 17.6% yet did not affect ANPP in the second compositional state (Figure 4c,d; Table 1). Warming did not affect ANPP in either of the two compositional states (Figure 4e,f; Table 1). Furthermore, mixed-effect model showed that $C_4$% is a major factor accounting for the interannual variation in the natural log response ratio of ANPP (Ln rr) to altered precipitation (double precipitation: $F_{1,53} = 7.28$, $p = 0.009$; halved precipitation: $F_{1,53} = 3.02$, $p = 0.088$; Table 2).

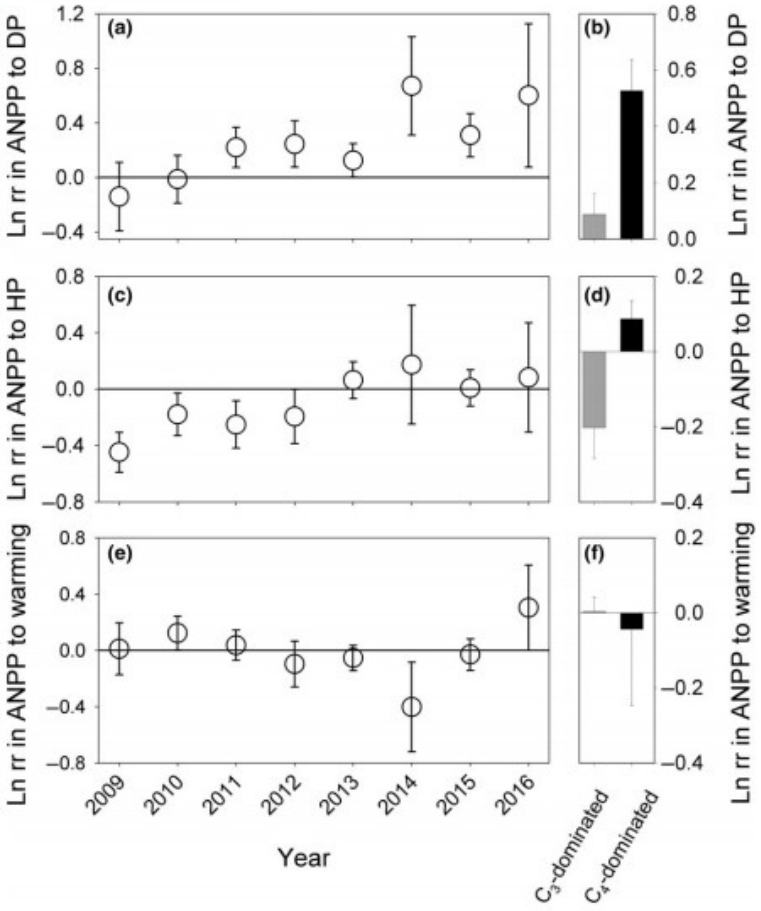


**FIGURE 4** Long-term shift in the natural log response ratio of aboveground net primary productivity (ANPP) to climate change. Interannual variation in natural log response ratio (Ln rr) of ANPP to DP, double precipitation (a) showed significant difference between the two compositional states (b), interannual variation in Ln rr of ANPP to HP, halved precipitation (c) showed significant difference between the two compositional states (d), and interannual variation in Ln rr of ANPP to warming (e) showed no difference between the two compositional states (f). Each point represents mean and standard error of the mean across replicates ($n$ = 8 for precipitation treatments and $n$ = 12 for warming treatment). Note that the $C_3$-dominated community was within 2009–2013 and the $C_4$-dominated community was within 2014–2016. See Table 1 for statistical results

**TABLE 1** Results ($p$ values with $F$ values in the brackets) of repeated-measures ANOVA for the responses of aboveground net primary productivity (ANPP), $C_3$ biomass and $C_4$ biomass to warming (W), altered precipitation (PPT), year and their interactions within 2009–2013 ($C_3$-dominated) and 2014–2016 ($C_4$-dominated), respectively. $p$ Values smaller than 0.05 are in bold

| | $C_3$-dominant | | | | $C_4$-dominant | | | |
|---|---|---|---|---|---|---|---|---|
| | *df* | ANPP | $C_3$ | $C_4$ | *df* | ANPP | $C_3$ | $C_4$ |
| W | 1, 15 | 0.903 (0.02) | 0.382 (0.81) | 0.386 (0.80) | 1, 15 | 0.802 (0.06) | **0.045 (4.77)** | 0.294 (1.18) |
| PPT | 2, 15 | **0.011 (6.13)** | 0.175 (1.96) | **0.031 (4.41)** | 2, 15 | **0.011 (6.23)** | 0.066 (3.28) | **0.001 (11.18)** |
| W × PPT | 2, 15 | 0.193 (1.84) | 0.133 (2.32) | 0.622 (0.49) | 2, 15 | 0.590 (0.55) | 0.690 (0.38) | 0.723 (0.33) |
| Year | 4, 72 | **<0.001 (11.35)** | **<0.001 (18.32)** | **0.038 (2.69)** | 2, 36 | **<0.001 (23.00)** | **<0.001 (14.50)** | **<0.001 (10.89)** |
| W × Year | 4, 72 | 0.516 (0.82) | 0.726 (0.51) | 0.643 (0.63) | 2, 36 | 0.755 (0.28) | **0.014 (4.86)** | 0.887 (0.12) |
| PPT × Year | 8, 72 | 0.625 (0.78) | 0.206 (1.41) | 0.987 (0.22) | 4, 36 | 0.913 (0.24) | **0.024 (3.19)** | 0.684 (0.57) |
| W × PPT × Year | 8, 72 | 0.850 (0.50) | 0.401 (1.06) | 0.876 (0.47) | 4, 36 | 0.341 (1.17) | 0.343 (1.16) | 0.482 (0.89) |

**TABLE 2** Effects of warming (W), proportion of $C_4$ biomass ($C_4$%), annual precipitation (PPT), and annual mean temperature (Tair) on the natural log response ratio of aboveground net primary productivity (Ln rr) under double precipitation and halved precipitation treatments

| Effect | *df* | *F* value | Pr > *F* |
|---|---|---|---|
| Ln rr, double precipitation | | | |
| W | 1, 6 | 1.66 | 0.245 |
| C4% | 1, 53 | 7.28 | 0.009 |
| PPT | 1, 53 | 1.03 | 0.315 |
| Tair | 1, 53 | 0.21 | 0.650 |
| Ln rr, halved precipitation | | | |
| W | 1, 6 | 0.32 | 0.594 |
| C4% | 1, 53 | 3.02 | 0.088 |
| PPT | 1, 53 | 0.03 | 0.872 |
| Tair | 1, 53 | 0.14 | 0.711 |

We also examined how the two functional groups responded to climate change in the two compositional states. In the first state (2009–2013), double precipitation increased $C_4$ plant growth by 31.3% on average ($p = 0.036$) but did not affect $C_3$ biomass ($p = 0.19$; Figure 5; Table 1); halved precipitation decreased $C_3$ biomass with a marginal significance by 21.7% on average ($p = 0.07$) but did not affect $C_4$ biomass ($p = 0.64$; Figure 5; Table 1); warming did not influence either $C_3$ or $C_4$ biomass (Table 1). In the second state (2014–2016), double precipitation increased $C_4$ biomass by 69.6% on average ($p = 0.001$; Figure 6a), but surprisingly reduced $C_3$ plant growth by 75.6% in the $C_4$-dominated community in the wettest year (i.e., 2015; Figure 6b; Table 1); halved precipitation did not have an impact on either $C_3$ or $C_4$ biomass (Figure 6b; Table 1); warming enhanced $C_3$ plant growth by 162% times in the wettest year (Figure 6c; Table 1).

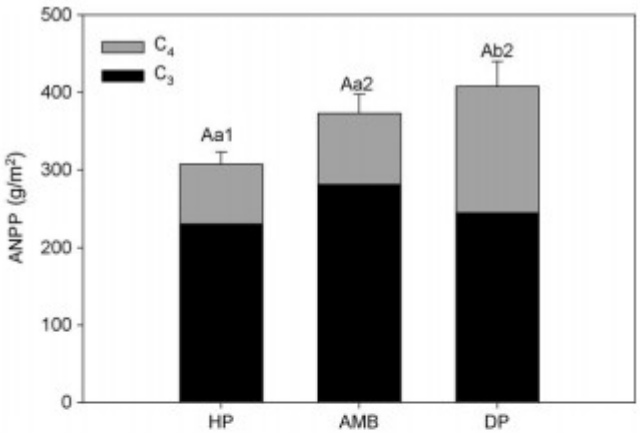


**FIGURE 5** Responses of total aboveground net primary productivity (ANPP) and biomass of the functional groups to climate change within 2009–2013. Different letters or numbers represent significant difference among treatments at $\alpha = 0.05$. Uppercases are for $C_3$ biomass, lowercases are for $C_4$ biomass and numbers are for total ANPP. *p* Values for the multiple comparisions in ANPP between the three precipitation treatments are (AMB vs. DP: 0.25; AMB vs. HP: 0.04; DP vs. HP: 0.0036); comparisions in $C_3$ biomass (AMB vs. DP: 0.19; AMB vs. HP: 0.07; DP vs. HP: 0.59); comparisons in $C_4$ biomass (AMB vs. DP: 0.036; AMB vs. HP: 0.64; DP vs. HP: 0.014). AMB is ambient precipitation, DP is double precipitation, and HP is halved precipitation. Gray bars are $C_4$ biomass, and black bars are $C_3$ biomass. See Table 1 for statistical results

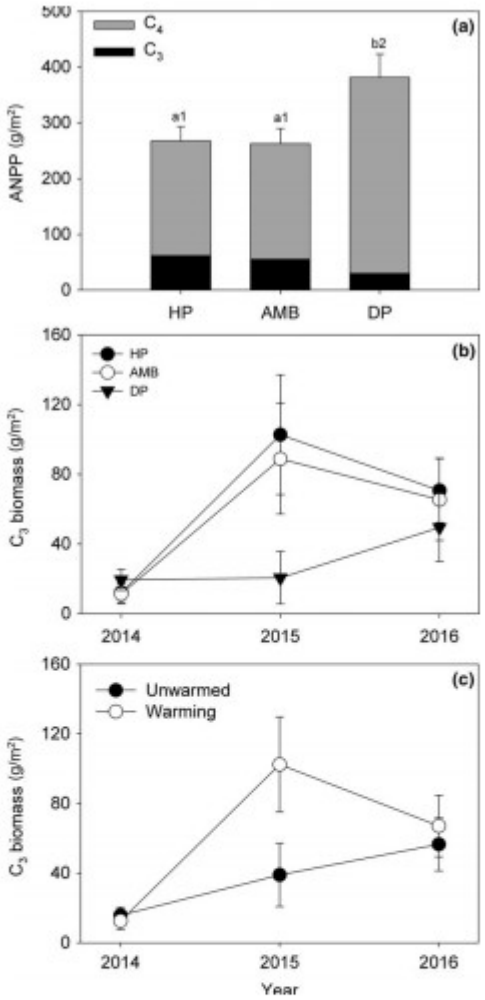


**FIGURE 6** Responses of total aboveground net primary productivity (ANPP) and biomass of the functional groups to climate change within 2014–2016. *p* Values for the multiple comparisions in ANPP between the three precipitation treatments are (AMB vs. DP: 0.007; AMB vs. HP: 0.89; DP vs. HP: 0.0092); comparisons in $C_4$ biomass (AMB vs. DP: 0.001; AMB vs. HP: 0.96; DP vs. HP: 0.0009). Double precipitation increased ANPP through positive effect on $C_4$ biomass (a, gray bars are $C_4$ biomass and black bars are $C_3$ biomass). In panel a, different letters or numbers represent significant difference among treatments at $\alpha = 0.05$. Lowercases are for $C_4$ biomass and numbers are for total ANPP. Double precipitation decreased $C_3$ biomass in 2015 (b) and warming increased $C_3$ biomass in 2015, the wettest year (c). In panel (a), AMB is ambient precipitation, DP is double precipitation, and HP is halved precipitation; in panel (b), solid circles represent halved precipitation, open circles are ambient precipitation, and triangles are double precipitation. In panel (c), open circles represent warming, and solid circle represent unwarmed treatment. See Table 1 for statistical results

# 4 DISCUSSION

## 4.1 Successional change in plant community

Our findings reveal the compositional state shift in the two plant functional groups over the eight experimental years. The studied temperate grassland transitioned from a $C_3$-dominant to a $C_4$-dominant system. The temporal

trends in $C_4$ and $C_3$ biomass may be explained by the removal of the disturbance, that is, grazing (Knapp & Medina, 1999; Koerner et al., 2014). The recent enclosure in 2008 has kept the experimental site from herbivore grazing, which weakens the top down effects on the plant community (Koerner et al., 2014; Post & Pedersen, 2008; Suttle, Thomsen, & Power, 2007) and thus shifts the plant community from one state to another, a successional change. Specifically, $C_3$-dominated communities in the early state were mostly composed of annual forbs, including *Ambrosia trifida* (giant ragweed), *Solanum carolinense* (horsenettle), and *Euphorbia dentate* (toothed spurge), which were all weedy and generally unpalatable plant species. Removal of grazing released the dominant palatable $C_4$ grasses, including *Tridens flavus* (Purpletop) and the invasive *Sorghum halepense* (Johnson grass) from herbivore control with consequent spread.

The community shift from annual weedy grass (e.g., *Bromus japonicus*) and annual forbs (e.g., *Ambrosia trifida*) to mostly perennial bunch grass (e.g., *Tridens flavus* and *Sorghum halepense*) is consistent with other studies in grassland succession (Booth, 1941; Odum Eugene, 1960; Perino & Risser, 1972). For example, reduced foliage herbivory resulted in large increases in perennial grass growth and reduction in forb abundance (Brown & Gange, 1992). The fact that the same $C_3$ species are still dominating the plant community nearby under ambient conditions (i.e., grazed condition), and that an adjacent long-term experimental site which was fenced from grazing for over four decades features a $C_4$-dominated community (Shi et al., 2016), indirectly supporting the grazing mechanism. The negative correlation between $C_3$ biomass and $C_4$ biomass further reveals possible antagonistic interaction at the functional group level, which can explain the opposite temporal trends in $C_3$ versus $C_4$ biomass. Another mechanism could also account for the temporal trend in functional group is that the removal of grazing may reduce soil nitrogen availability (Mcneil & Cushman, 2005) and lead to dominance of $C_4$ plant species, which can utilize nitrogen more efficiently than $C_3$ species (Lambers et al., 1998). And it could also just be a release from grazers that preferentially choose the $C_4$ grasses over the less desirable $C_3$ forbs.

In addition, the abrupt shift from $C_3$ dominance to $C_4$ dominance during the study period happened in year 2014 which was extremely dry in terms of annual rainfall and soil water content. The sudden change in the compositional state suggests that the extreme dry year might have accelerated the rate of the successional change. This hypothesis is consistent with the result that halved precipitation treatment negatively affects the $C_3$ functional group. Besides dry year 2014, the wet years of 2015 and 2016 may have favored $C_4$ perennials over $C_3$ annuals. Without the extreme years, the plant community may have slowly converged to this $C_4$-dominated state, and this succession was sped up by an extreme event.

## 4.2 Responses of ANPP to climate change: long-term shift and associated mechanisms

We expected long-term shift in the responses of ANPP to climate change due to the documented transition from $C_3$- to $C_4$-dominated plant community (Langley & Megonigal, 2010; Morgan et al., 2011; Zelikova et al., 2014). Consistent with our prediction, amplified response of ANPP to double precipitation and dampened response of ANPP to halved precipitation were observed.

In the first compositional state (dominated by $C_3$ species), drought reduced ANPP through adversely influencing $C_3$ biomass and double precipitation increased $C_4$ biomass, as predicted by physiology. It could also be because $C_3$ species as annuals and $C_4$ species as perennials had differential sensitive to precipitation change. However, the increase in $C_4$ biomass was not proportionally enough to make a significant impact on the total ANPP. The strong competition between $C_3$ and $C_4$ in double precipitation treatment may account for a lack of response in ANPP to double precipitation in the first state. The findings are partially consistent with meta-analyses (Wilcox et al., 2017; Wu, Dijkstra, Koch, Penuelas, & Hungate, 2011) which report positive and negative responses of ANPP to increased and decreased precipitation, respectively.

Altered sensitivity of ANPP to precipitation change in the second compositional state (dominated by $C_4$ species) in our study supports long-term shift in precipitation sensitivity (Smith et al., 2009; Wilcox et al., 2016). Double precipitation greatly increased the ANPP by enhancing $C_4$ biomass. Yet, halved precipitation did not reduce ANPP, which likely results from the well adaptations of the dominant $C_4$ plant species to dry conditions (Ehleringer et al., 1997; Epstein et al., 2002). In contrast to our expectation, halved precipitation did not affect $C_3$ biomass in the $C_4$-dominated community, possibly due to the fact that dry conditions may reduce interspecific competition (Kardol et al., 2010) and alleviate the pressure on $C_3$ from $C_4$. Unexpected is also that increased precipitation reduced $C_3$ plant growth (Wilcox et al., 2017; Wu et al., 2011) in the $C_4$-dominated community in the wettest year (year 2015), likely due to the biotic competition with $C_4$ species that benefited from increased precipitation, highlighting the interactive nature of mechanisms that regulate climate sensitivity of ecosystem functions. In addition, $C_3$ species in this study are mostly annuals which are weak competitors compared to perennials.

We also predicted that the plant community in the second compositional state ($C_4$ dominated) would show greater positive response to warming given that $C_4$ plants are considered to be better adapted to warmer climates (Morgan et al., 2011) than $C_3$ herbaceous plants. Instead, warming did not affect ANPP in either of the two states. The neutral response of ANPP to warming in the $C_3$-dominated community may be explained by the limited change in soil water content induced by warming and the relative

insensitivity of $C_3$ plants in our studied community to warming; while the lack of response to warming and warming-caused desiccation in the $C_4$-dominated community may be explained by the fact that $C_4$ species are well adapted to drought. This finding is consistent with the results from a semiarid mixed-grass prairie showing that ANPP was unaffected by 4 years of warming (Morgan et al., 2011). A similar finding was also reported in an old field plant community, where warming did not affect the ANPP of the $C_3$-dominated system (Hoeppner & Dukes, 2012). In terms of individual responses of plant functional groups, warming did not affect $C_3$ or $C_4$ biomass in the first compositional state ($C_3$-dominant community). However, warming enhanced $C_3$ plant growth in the wettest year (2015) when the community was dominated by $C_4$ species. This supports that warming is likely to interact with extreme rainfall condition to exert impact on plant growth water availability (Jentsch, Kreyling, & Beierkuhnlein, 2007; Smith et al., 2009).

Previous research has demonstrated various temporal trends in climate sensitivity of ecosystem functions. Amplified trends of soil C fluxes to warming was observed in both terrestrial (Xu et al., 2015) and aquatic ecosystems (Yvon-Durocher et al., 2017); attenuated trends of ecosystem functions such as (aboveground net primary productivity) ANPP and soil respiration to warming were also found in both grassland (Wu et al., 2012) and forest ecosystems (Melillo et al., 2002). So were the lack of temporal trends to climate change (Mueller et al., 2016; Zelikova et al., 2014; Zhu, Chiariello, Tobeck, Fukami, & Field, 2016). Results of this study showed all possible scenarios of the altered sensitivity of ecosystem productivity to long-term climate change: amplified sensitivity to increased precipitation, dampened sensitivity to decreased precipitation, and lack of response to warming over time. In contrast to previous identified mechanisms, we found strong evidence that successional change in plant community was the contributing mechanism behind both the amplified and dampened responses.

Overall, the altered sensitivity of ANPP to precipitation change and the lack of response of ANPP to long-term warming highlight the predominant role of water availability in driving grassland ecosystem responses. The primary role of water—not temperature—is consistent with a global climate sensitivity study, in which precipitation sensitivity is predominant in grassland ecosystems (Seddon, Macias-Fauria, Long, Benz, & Willis, 2016). In addition, the diverse responses of plant functional group biomass to climate change suggest that, besides plant physiology, there are other dominant factors such as biotic competition moderating long-term ecosystem responses, emphasizing the complexity of ecosystem responses to climate change.

Our findings have significant implications for understanding the linkage between plant community and ecosystem functioning in the context of long-term climate change. First, altered climate sensitivity with transition in the functional group composition highlights the importance of understanding the mechanisms underlying such a compositional state shift and the significance

of involving vegetation dynamics in predicting future carbon state. Second, if climate change would affect species composition in the future (Cramer et al., 2001; Ehleringer et al., 1997; Epstein et al., 2002), shift in species composition could in turn act as a long-term feedback to alter the ecosystem responses to climate change. In addition, long-term climate change experiments in early successional systems are essential for understanding the changes in strength and direction of ecosystem responses to climate change (Kröel-Dulay et al., 2015).

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